

# Introduced deer and the pollination and reproduction of an animal-pollinated herb

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**Abstract:** We evaluated the hypothesis that the modified population density of *Aquilegia formosa* Fisch. ex DC. (Ranunculaceae) resulting from the introduction of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in the Haida Gwaii archipelago affects the pollination and reproductive performance of this herbaceous species. We compared the population density, pollination, and reproductive success of *A. formosa* among three small islands colonized by deer and three deer-free islands. Islands with deer had a substantially lower absolute density and a greater relative density of *A. formosa* than deer-free islands. The presence of deer was associated with higher pollen deposition, which probably resulted from the greater relative density of *A. formosa* on islands with deer. However, the presence of deer had no significant effect on individual reproductive success. The latter result is likely a consequence of the lack of pollen limitation in this species, as well as of the conflicting relationship between the absolute and relative densities of *A. formosa* and the presence of deer.

**Key words:** introduced deer, pollination and reproduction of a herb pollinated by animals, *Aquilegia formosa*.

**Résumé :** Nous avons examiné l'hypothèse que la modification des densités d'*Aquilegia formosa* Fisch. ex DC. (Renonculacées) qui a suivi l'introduction du cerf à queue noire (*Odocoileus hemionus sitkensis*) sur l'archipel de Haïda Gwaii était susceptible d'affecter la pollinisation et les performances reproductives de cette plante herbacée. Nous avons comparé les densités de population, la pollinisation et le succès reproducteur entre des îles colonisées par le cerf et des îles sans cerfs. Sur les îles avec cerfs, les densités absolues d'*A. formosa* étaient inférieures, et ses densités relatives supérieures aux valeurs observées sur les îles sans cerfs. En présence de cerf, la déposition de pollen de l'espèce était plus élevée, un résultat probablement lié à la plus forte densité relative d'*A. formosa* sur ces îles. Par contre, la présence de cerf n'avait pas d'effet significatif sur le succès reproducteur. Ceci s'explique probablement par l'absence de limitation en pollen chez cette espèce et par la réponse opposée de la densité absolue et relative d'*A. formosa* à la présence de cerfs.

**Mots-clés :** cerf introduit, pollinisation et reproduction d'une herbacée à pollinisation animale, *Aquilegia formosa*.

## Introduction

Biological invasions are one of the most serious threats to biodiversity worldwide. Although many nonindigenous species have only minor effects on their recipient communities, some have drastic effects on species composition, habitat structure, and ecosystem processes (Elton 1958; Williamson 1996; Lockwood et al. 2006). Large mammalian herbivores figure prominently among the latter (de Vos et al. 1056; Ebenhard 1988; Hobbs 1996; Vázquez 2002). In this paper, we evaluate the effects of an introduced ungulate, Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), on the pollination and reproduction of a herbaceous plant in the Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia, Canada). Black-tailed deer, originally native to

mainland North America, have been introduced to Graham Island in the north of Haida Gwaii. Deer have later dispersed to smaller islands in the proximity of the main islands, but have not yet colonized a handful of the most isolated islands. This situation provides an opportunity to study the effects of black-tailed deer on the biota of Haida Gwaii in a replicated natural experiment, and a whole research program has developed to make use of this opportunity (see, e.g., Martin and Baltzinger 2002; Vourc'h et al. 2002a, 2002b; Martin and Joron 2003; Vila et al. 2004a, 2004b; Allombert et al. 2005a, 2005b; Stroh et al. 2008; Martin et al. 2009).

Herbivores can frequently affect plant population density (Crawley 1997), which in turn can result in an Allee effect

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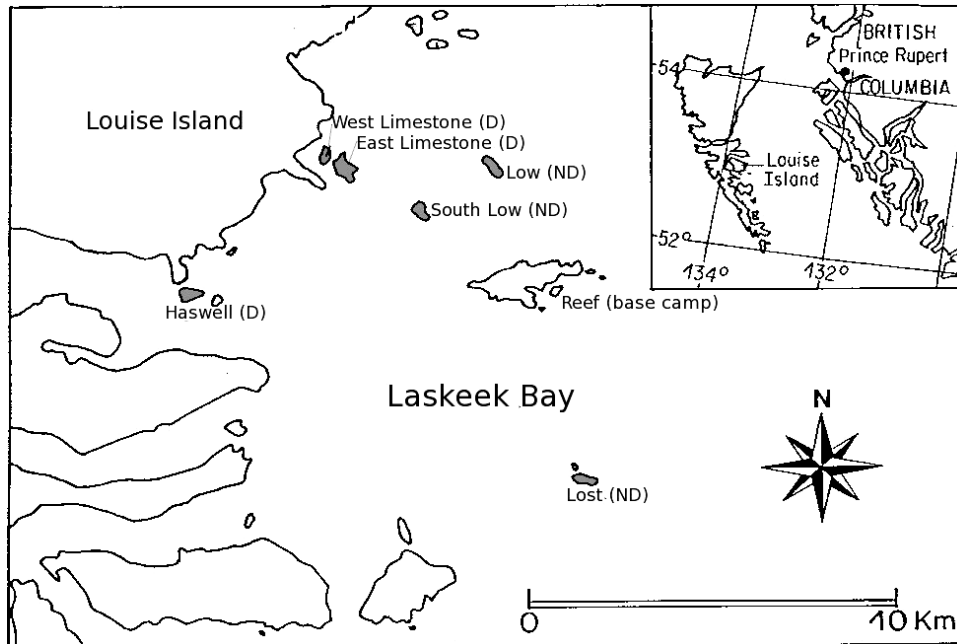
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**Fig. 1.** Map of Laskeek Bay showing islands included in the study (highlighted in grey). D, islands with deer; ND, deer-free islands.



(Allee et al. 1949; Courchamp et al. 1999, 2008; Stephens and Sutherland 1999), so that plants at low densities experience greater pollination limitation and lower reproductive success than plants at higher densities. The Allee effect can exacerbate the direct effect of herbivores on the density of plant populations, further reducing their population growth rate and increasing their likelihood of extinction (Groom 1998; Hackney and McGraw 2001). This effect can occur through at least two alternative mechanisms (Vázquez and Simberloff 2004; Ghazoul 2005; Aizen and Vázquez 2006; Traveset and Richardson 2006; Vázquez 2007). First, decreased “absolute” plant population density (i.e., the density of a focal plant species irrespective of the density of other species) can lead to decreased pollinator visitation frequency and lower pollen deposition (i.e., an effect on the “quantity” of pollination). Second, decreased “relative” plant population density (i.e., density of conspecifics relative to density of all species visited by pollinators) can lead to decreased conspecific and increased heterospecific pollen deposition in stigmas per pollinator visit (thus affecting the “quality” of pollination). Of course, usually both absolute and relative densities will vary simultaneously. If they both change in the same direction, we expect reproductive success to be affected simultaneously through lower quantity and lower quality of pollination. However, if absolute and relative densities change in opposite directions (e.g., the former decreases while the latter increases, which may happen when a plant species persists in habitat refuges inaccessible to herbivores where other plants cannot grow), the net effect of herbivores on plant pollination and reproduction will be weaker or nil.

Our study focused on *Aquilegia formosa* Fisch. ex DC. (Ranunculaceae), a short-lived, hummingbird-pollinated (Grant 1992), perennial herbaceous species distributed throughout western North America (Pojar and MacKinnon

1994), whose abundance is drastically reduced in islands with deer. Although *A. formosa* is probably self-compatible (as all other species in its genus studied to date; Miller 1978; Eckert and Schaefer 1998), and flowers open sequentially within an individual plant, it is protandrous, and only a small fraction of flowers in a plant are open at a given moment (authors’ personal observation), which may increase its dependence on cross-pollination for reproduction.

The above arguments and the reproductive characteristics of *A. formosa* led us to hypothesize that if reproduction of *A. formosa* were pollen-limited, its reproductive output would be likely to suffer from deer-caused decreased population density. We predicted that if both absolute and relative densities of *A. formosa* decreased in deer islands, its reproductive success would be lower than in deer-free islands because of lower quantity and quality of pollination. However, if absolute and relative densities changed in opposite directions, the effect of deer presence on pollination and reproduction would be weak or nonexistent. To evaluate these predictions, we addressed the following questions: How do absolute and relative densities of *A. formosa* respond to the presence of deer? Does the effect of deer on relative and absolute densities of *A. formosa* affect the quantity and (or) quality of pollen deposited in stigmas? Is the reproduction of *A. formosa* pollen-limited? If there is pollen limitation of reproduction, does the effect of deer on the density of *A. formosa* result in an indirect effect on reproductive success?

## Methods

### Study sites

We worked in small islands in the southeastern area of the Haida Gwaii archipelago. We selected three islands that have never been colonized by deer (Low, South Low, and

**Table 1.** Percent cover and frequency of *Aquilegia formosa* in shoreline plots in study islands.

Island	Percent cover	Frequency
<b>Deer present</b>		
Haswell	0.0000±0.0000	0
West Limestone	0.0000±0.0000	0
West Skedans	0.0000±0.0000	0
<b>Deer absent</b>		
Low	0.0005±0.0005	5
Lost	0.1005±0.3160	6
South Low	0.2005±0.3160	6

**Note:** Because we had no density estimates for East Limestone, we show instead data from another island, West Skedans.

Lost) and three islands that have been colonized by deer for at least 50 years (East Limestone, West Limestone, and Haswell; Fig. 1).

### Density estimation

In the context of plant–pollinator interactions, cover is a better estimate of floral density than counts of individuals, because individuals may vary greatly in the number of flowers. Thus, we used percent cover of *A. formosa* as a measure of flower density in our study islands. Cover estimates come from Stockton et al. (2005). These authors measured the percent cover in 10 (per island) randomly spaced, circular plots of 10 m radius, in shoreline habitats at the forest edge; the type of habitat where *A. formosa* is normally found. Note that because we had no density estimates for East Limestone, we show instead data from another island, West Skedans; our casual observations during the pollination studies indicate that the density in East Limestone was comparable with other deer-free islands.

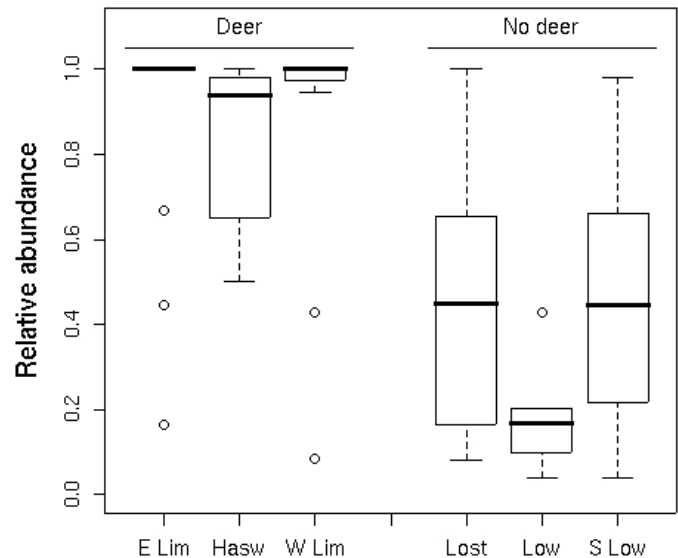
Relative density was estimated at the neighborhood level, the scale appropriate for pollinator foraging decisions. We used circular plots of 2 m radius centered at the plant on which pollination and reproductive measurements were conducted (see below). Individual plants to be sampled were selected randomly, attempting to sample as many individuals in as many locations within each island as possible. In each plot, we recorded the number of flowering individuals, as well as the number of open flowers of *A. formosa*, and the number and identity of flowering individuals of other animal-pollinated species. Relative density is thus defined as the number of flowers of *A. formosa* within the plot divided by the total number of flowers of any species (including *A. formosa*) within that plot.

### Pollination and reproductive success

#### Pollination

Pollination performance of plants was evaluated by quantifying the number of conspecific and heterospecific pollen grains deposited on stigmas. As we mentioned above, individual plants to be sampled were selected randomly, attempting to sample as many individuals in as many locations within each island as possible, to minimize spatial autocorrelation among samples (range of sample sizes: 7–40 individuals per island). Stigmas of up to five flowers of the

**Fig. 2.** Relative density of *Aquilegia formosa* in study islands, measured at the floral neighborhood level. Horizontal line dividing each box in two indicates the median; box limits are the first and third quartiles of the distribution; whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range from the box; circles indicate outlying data points falling beyond whisker limits. The best fitting model did not include “Island” as random factor, Table 3; fixed effect of deer on relative density:  $F_{[1,111]} = 69.75$ ;  $P < 0.001$ .



same individual plant were excised, placed on microscope slides, stained with a drop of Alexander’s stain, and covered with a cover slip (see Kearns and Inouye 1993). Conspecific and heterospecific pollen grains were counted under a microscope.

#### Reproductive success

Individuals of *A. formosa* were randomly selected from each island to estimate the fruit and seed set per flower and per plant. Plants were tagged with flagging tape, recording the total number of flower buds, open flowers, and senescent flowers (range of sample sizes: 23–40 plants per island). Once the fruits had developed, the number of fruits and seeds per fruit in marked branches were counted. Three reproductive variables were estimated with these data: fruit set (proportion of tagged flowers that set fruit), seeds per ovule, and seed output per plant (number of seeds per fruit × total number of flowers in the plant × the proportional fruit set).

#### Evaluation of pollen limitation

Because the lower reproductive success on islands with deer could be caused by lower resource availability on these islands, rather than poorer pollination performance, it is important to evaluate the extent to which reproduction is pollen-limited. To this end, we conducted observational and experimental studies of pollen limitation.

Observational studies considered data on natural pollen deposition and the three reproductive variables described above. If reproduction were pollen-limited, we predicted a positive relationship between conspecific pollen deposition on stigmas and reproductive success.

**Fig. 3.** Reproductive output of *Aquilegia formosa* versus number of conspecific grains deposited in stigmas by natural pollination: (a) proportional fruit set:  $R^2 = 0.01$ ,  $F_{[1,111]} = 1.31$ ,  $P = 0.25$ ; (b) number of seeds per ovule:  $R^2 = 0.01$ ,  $F = 0.84$ ,  $P = 0.36$ ; (c) number of seeds per plant:  $R^2 = 0.02$ ,  $F_{[1,111]} = 2.56$ ,  $P = 0.11$ .

**Table 2.** Habitat types of individuals of *Aquilegia formosa* on which pollination and reproductive variables were measured.

Habitat type	Deer absent	Deer present
Cliff		61
Limestone pocket	1	7
Meadow	30	0
Flat rocky substrate	55	15

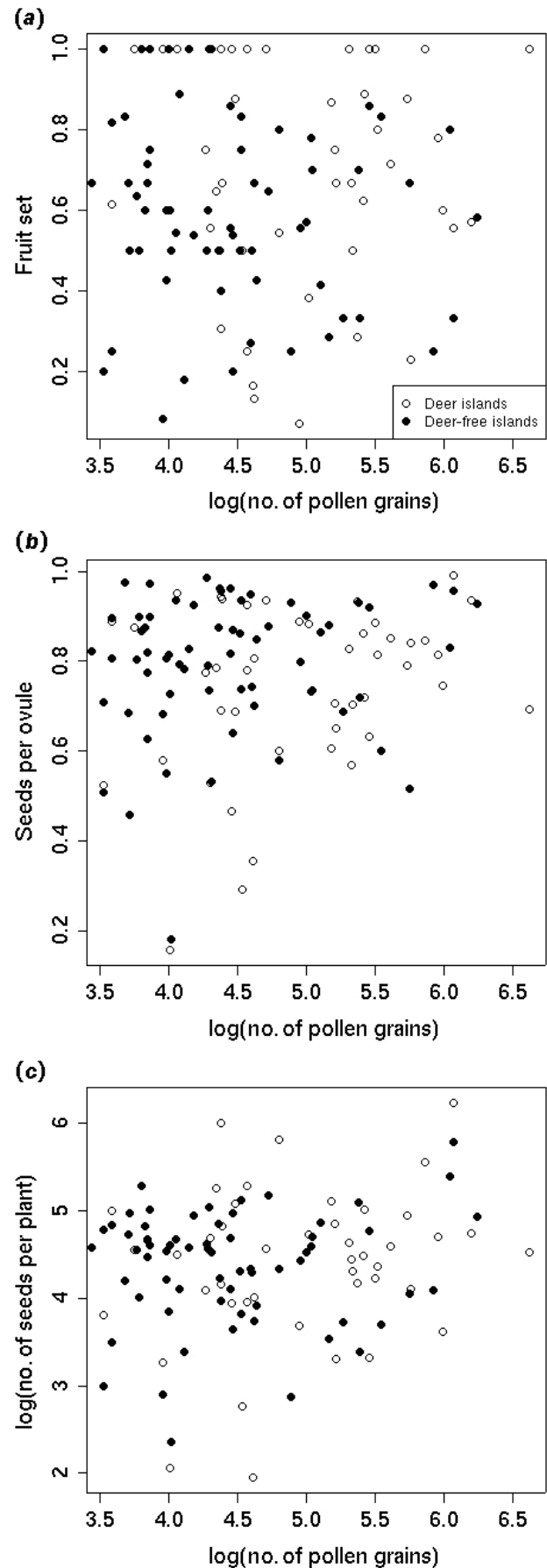
**Note:**  $\chi^2$  test of independence of between habitat type and deer presence:  $\chi^2 = 76.44$ ;  $df = 3$ ;  $P < 0.001$ .

We conducted two sets of experimental studies of pollen limitation: (i) pollen supplementation and (ii) bagging. In pollen supplementation studies, we randomly selected paired experimental (pollen added) and control (no pollen added) plants in each island. We hand-pollinated roughly half of the open flowers of each experimental plant when we visited the island. Flowers of *A. formosa* open sequentially throughout the flowering season, which meant that only a few flowers were open at a given moment. Because traveling between islands was difficult, and bad weather prevented us from leaving the base camp for several days, we could visit most islands only once during the flowering season (with a second visit after flowering had ended to estimate fruit and seed production), thus missing many flowers produced by a particular plant throughout the flowering season. If reproduction were pollen-limited, we predicted a positive effect of pollen supplementation on seed production; we also expected a more strongly positive effect of pollen addition on reproduction in deer islands, where density is lower, than in deer-free islands. In addition to pollen supplementation, we bagged selected plants to exclude pollinators, so as to evaluate *A. formosa*'s ability for autonomous selfing.

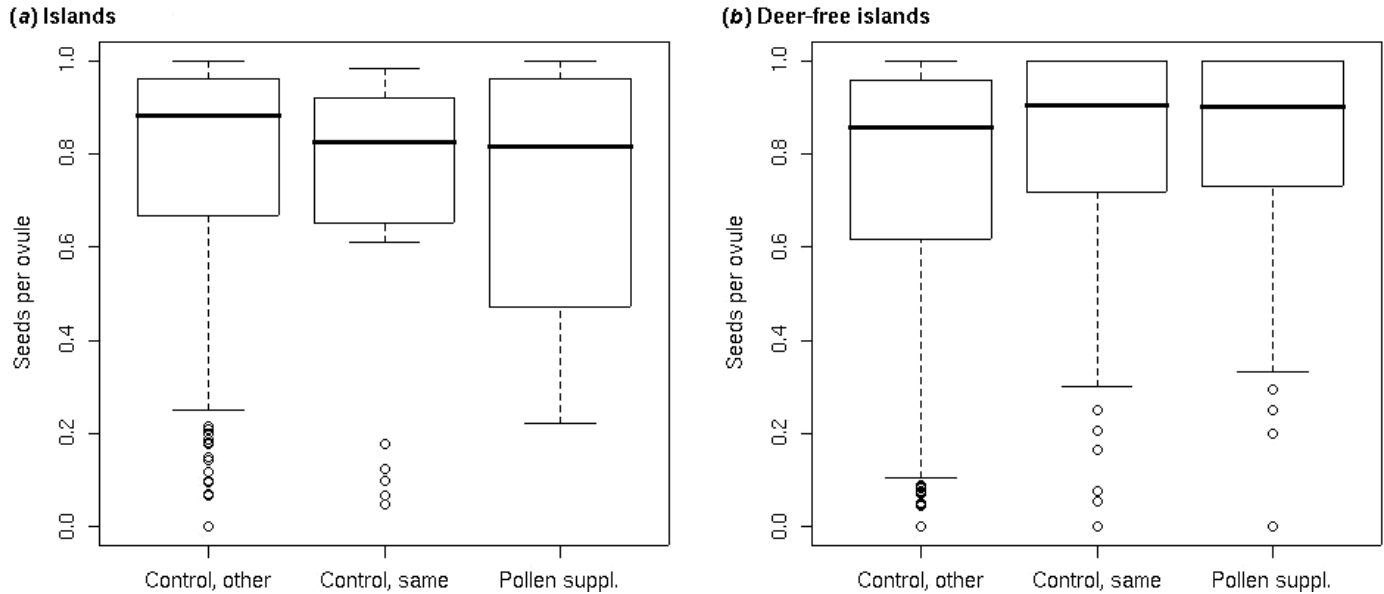
### Statistical analyses

Regressions between number of conspecific pollen grains and pollination and reproductive variables were conducted with the `lm` function of R statistical software (R Development Core Team 2007). Numerical variables were log-transformed for analyses to achieve normality of errors, except proportional fruit set, which was arcsine square root transformed.

The effect of pollen supplementation and deer on pollination and reproductive variables was analyzed with linear fixed and mixed models, which differed in the inclusion of "Island" as a random factor (i.e., a fixed model was nested within a more general mixed model; see Table 3 for model details). For a given response variable, we used Akaike's information criterion (AIC) to compare between models with and without the random factor Island; we report the differential AIC (dAIC), the difference between each alternative model and the best fitting one (dAIC = 0 for the best fitting



**Fig. 4.** Effect of pollen supplementation on the number of seeds per ovule produced by *Aquilegia formosa*. Labels in the abscissa indicate pollination treatments: Pollen suppl., flowers that received supplemental pollen; Control, same, flowers with no pollen addition in plants that received supplemental pollen; Control, other, flowers with no pollen addition in unmanipulated plants. The best fitting model did not include “Island” or the “Island × Pollen” supplementation interaction as random factors (Table 3); fixed effect of pollen supplementation:  $F_{[2,2124]} = 0.89$ ,  $P > 0.1$ ; fixed effect of deer:  $F_{[2,2124]} = 3.34$ ,  $P > 0.05$ ; effect of number of ovules (covariable):  $F_{[1,2124]} = 53.06$ ,  $P < 0.001$ . Conventions as in Fig. 2.



**Table 3.** Selection of linear models describing the effect of deer on relative density, pollination, and reproduction of *Aquilegia formosa* (best fitting models are those with the differential Akaike’s information criterion (dAIC) = 0).

Response variable	Fixed factor	Random factor	Covariable	dAIC
Relative density	Deer			0
Relative density	Deer	Island		8.39
Conspecific pollen	Deer			0
Conspecific pollen	Deer	Island		3.82
Heterospecific pollen	Deer			5.82
Heterospecific pollen	Deer	Island		0
Fruit set	Deer			11.18
Fruit set	Deer	Island		0
Seeds per ovule	Deer		Ovules	0
Seeds per ovule	Deer	Island	Ovules	22.68
Seeds per plant	Deer		Flowers	0
Seeds per plant	Deer	Island	Flowers	9.16
Seeds per ovule	Pollen suppl., Deer		Ovules	0
Seeds per ovule	Pollen suppl., Deer	Island	Ovules	23.87
Seeds per ovule	Pollen suppl., Deer	Island, Pollen suppl. × Island	Ovules	9.96

model) (Burnham and Anderson 2002; Johnson and Omland 2004). For the best fitting model, we evaluated significance of fixed effects with either the  $F$  (fixed effects models) or  $t$  (mixed models) statistics (see Bates 2005, 2006). Analyses were conducted with the `lm` and `lmer` functions of R statistical software for the fixed and mixed models, respectively.

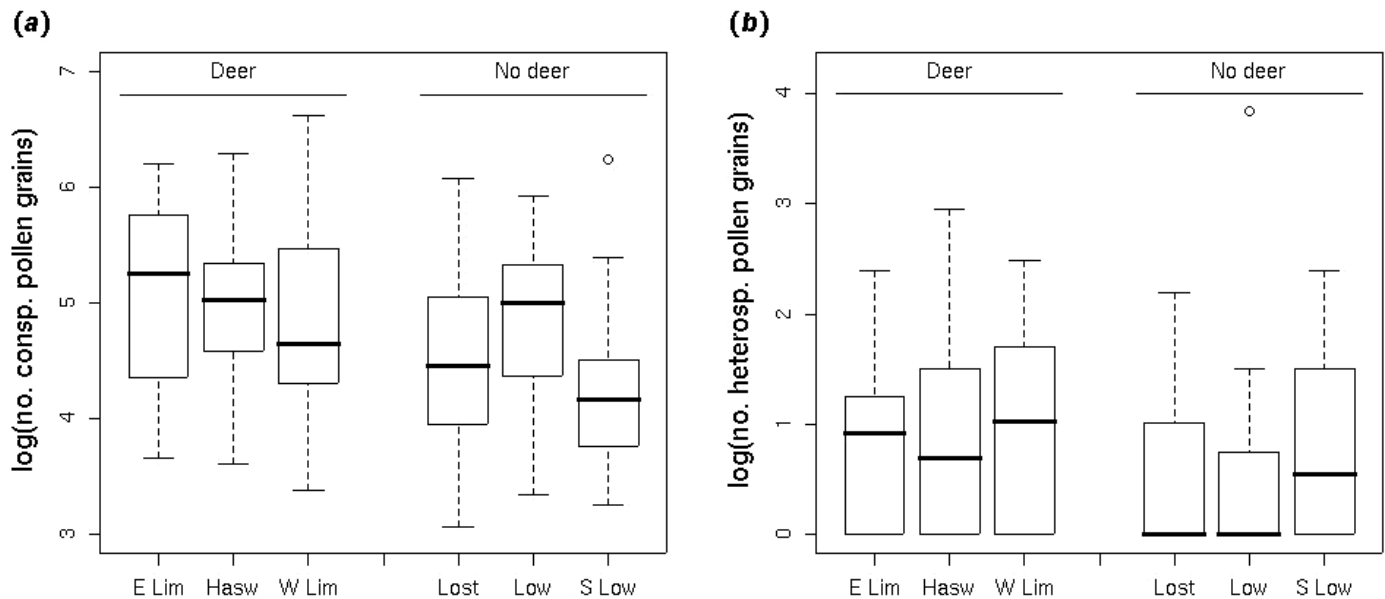
Histograms of residuals and quantile–quantile plots were visually assessed to evaluate deviations from normality. In all cases, variable transformations resulted in normalization of residuals.

## Results

### Deer presence and density of *Aquilegia formosa*

Deer presence resulted in a strong decrease in the density of *A. formosa* (Table 1). In contrast, relative density at the neighborhood level was significantly greater in deer islands than in deer-free islands (Fig. 2; Table 3). The individuals found in deer islands were mostly in marginal habitats such as cliff walls and holes in limestone fields, and virtually ab-

**Fig. 5.** Box plots showing the effect of deer presence on pollination in *Aquilegia formosa*. (a) Conspecific pollen deposition; the best fitting model did not include “Island” as random factor (Table 3); fixed effect of deer:  $F_{[1,111]} = 16.46$ ,  $P < 0.001$ . (b) Heterospecific pollen deposition; the best fitting model did not include “Island” as random factor (Table 3);  $F_{[1,111]} = 2.15$ ,  $P > 0.1$ . Conventions as in Fig. 2.



sent from flat substrates (meadows and flat rocky areas), the predominant habitat type of *A. formosa* in deer-free islands (Table 2). Thus, *A. formosa* in deer islands is rarer, is mostly restricted to more marginal habitats than in deer-free islands, and is in higher relative densities than in islands with deer.

### Pollen limitation

Bagging resulted in significantly lower seed set than open pollination (mean  $\pm 1$  SD of proportion of seeds per ovule: bagged,  $0.38 \pm 0.40$ ; unbagged,  $0.68 \pm 0.38$ ;  $t = 5.05$ ,  $df = 120.69$ ,  $p < 0.0001$ ). Thus, although *A. formosa* is able to produce seeds by autonomous selfing, animal pollination results in almost a twofold increase in seed production. However, there was no significant relationship between number of conspecific pollen grains received per stigma and any of the reproductive variables (Fig. 3). Likewise, pollen supplementation did not result in increased reproductive output, and this effect did not differ between deer and deer-free islands (Fig. 4; Table 3). Thus, variation in pollination levels does not appear to have a strong effect on the reproductive output in *A. formosa*, suggesting low pollen limitation of reproduction.

### Effects of deer presence on pollination and reproduction

There was a significant effect of deer presence on the number of conspecific pollen grains deposited on stigmas: conspecific pollen deposition tended to be greater in deer islands than in deer-free islands (Fig. 5a; Table 3). There was also a trend towards greater deposition of heterospecific pollen in deer islands, but this trend was not statistically significant (Fig. 5b; Table 3). There was no significant effect of deer on any of the reproductive variables (Fig. 6; Table 3).

## Discussion

Our results show that the density (measured here as cover) of *Aquilegia formosa* decreases while its relative density at the floral neighborhood increases in islands with deer. We also found no detectable pollen limitation of reproduction, even though animal pollination results in a twofold increase of reproductive success compared with pollinator exclusion. This lack of pollen limitation of reproduction combined with the conflicting effect of deer on the two components of density translated into only a weak effect of the presence of deer on pollen deposition and no detectable effect on reproductive success. Thus, in spite of having been almost wiped-out by deer, *A. formosa* is able to persist and reproduce successfully in isolation in habitat refuges such as cliff walls and limestone pockets.

There is one important caveat about the above results: our measures of reproductive performance did not take into account seed quality or viability. We worked on small islands, and thus low density means low effective population size; as a consequence, reproduction might be affected in the long run not only through the ecological mechanisms considered in our hypothesis but also through genetic mechanisms involving inbreeding depression (Mavraganis and Eckert 2001). In *Aquilegia canadensis*, a species closely related and morphologically similar to *A. formosa*, self-pollination does not provide reproductive assurance in terms of seed set, and any positive effect of self-pollination is greatly outweighed by severe seed discounting and inbreeding depression (Eckert and Schaefer 1998; Herlihy and Eckert 2002). It is at least possible that seeds produced by the isolated individuals of deer islands were more inbred, and thus more subject to inbreeding depression than those produced by individuals growing in denser patches of deer-free islands. This effect of inbreeding on reproductive performance could oc-

**Fig. 6.** Effect of deer presence on the reproduction of *Aquilegia formosa*. (a) Proportional fruit set (fruits per flower); the best fitting model included “Island” as random factor (Table 3); fixed effect of deer:  $t = 0.03$ ,  $P > 0.05$ . (b) Proportional seed set (seeds per ovule); the best fitting model did not include “Island” as random factor; fixed effect of deer:  $F_{[1,145]} = 1.17$ ,  $P > 0.05$ ; effect of number of ovules (covariable):  $F_{[1,145]} = 7.72$ ,  $P < 0.01$ . (c) Seeds per plant; the best fitting model did not include “Island” as random factor; fixed effect of deer:  $F_{[1,145]} = 0.40$ ,  $P > 0.05$ ; effect of number of ovules (covariable):  $F_{[1,145]} = 38.34$ ,  $P < 0.001$ .

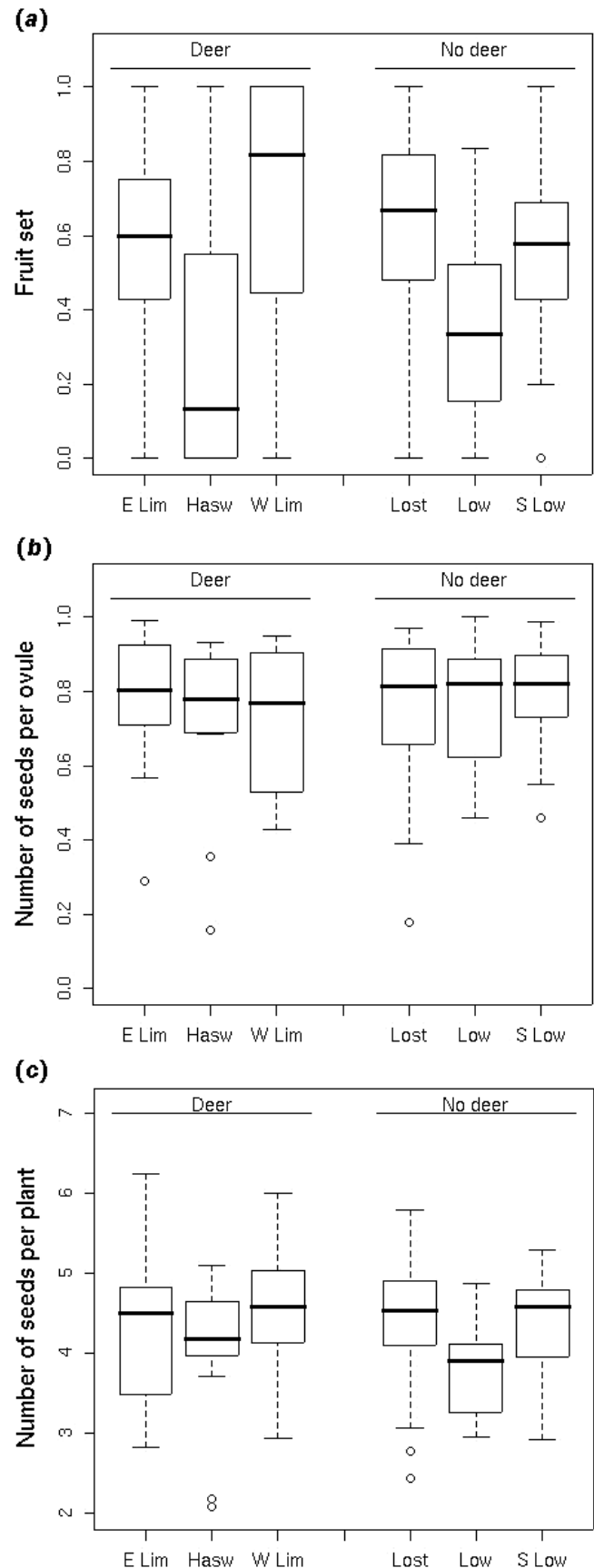
cur in spite of no effect on fruit or seed production. Future studies should evaluate this possibility with seed viability experiments.

Another important limitation of our study is that deer was distributed in a highly nonrandom pattern among our study island, being present in western islands close to the main island and absent in more remote, eastern islands. This segregated spatial pattern of deer presence could have influenced our results. This is in fact the biggest limitation of the so-called “field experiments”, in which “treatment” assignment to experimental units is not the result of planned experimental design but rather the result of unplanned natural occurrence. Regrettably, the nature of the ecological process we are studying (invasion by an ungulate and its potential disruption of plant–pollinator interactions), which occurs at large spatial and temporal scales, made it unfeasible for us to conduct experimental manipulation.

What are the broader implications of our study? Several features of plant–pollinator interactions seem to make them rather tolerant to perturbations (Bond 1994; Morris 2003; Memmott et al. 2004). Thus, the conditions, under which disruption of this type of mutualism is expected, are somewhat restricted, and many plants are not expected to suffer even from major disruptions in their plant–pollinator interactions. Thus, it comes as no surprise that a previous study of the indirect effects of introduced ungulates on pollination and reproduction found convincing evidence of such effects only for 1 of 11 species included in the study (Vázquez and Simberloff 2004). Deer and other introduced ungulates seem much more likely to influence native animal-pollinated plants directly by consumption or trampling than indirectly through the disruption of plant–pollinator interactions (Knight 2004).

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